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Punctuated Equilibria: A Critique[1,2])

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Introduction

A current controversy in evolutionary theory revolves around the concepts of punctuated equilibria and phyletic gradualism. The punctuated equilibrium concept is being promoted actively by a group of younger paleontologists, some of whom see a scientific revolution in the making.

There is no group actively opposed to punctuated equilibria, so far as I am aware; however, many evolutionists are skeptical about it and/or disagree with particular aspects. In general, evolutionists adhering to traditional views of macroevolution have been put on the defensive. A third amorphous faction consists of numerous biologists who are not involved in the controversy themselves but are curious about it and wonder what it is all about. A critical review of punctuated equilibria is needed and is offered here.

The basic papers on punctuated equilibria are ELDREDGE and GOULD (1972) and GOULD and ELDREDGE (1977) [cf. also ELDREDGE and CRACRAFT (1980)]. We will discuss the two basic papers first before we consider other later publications.

Phyletic Gradualism

The punctuational model is presented as "an alternative to phyletic gradualism" (ELDREDGE and GOULD, 1972, p. 82). Phyletic gradualism is the view that "new species arise from the slow and steady transformation of entire populations" (op. cit., p. 84, cf. also p. 89). "Under phyletic gradualism, the history of life should be one of *stately unfolding*. Most changes occur slowly and evenly by phyletic transformation; splitting, when it occurs, produces a slow and very gradual divergence of forms ..." (op. cit., p. 109, italics in original).

Furthermore, phyletic gradualism is presented as being the conventional view. "Paleontology's view of speciation has been dominated by the picture of 'phyletic gradualism'" (ELDREDGE and GOULD, 1972, p. 84). Gradualism "remains the 'official' position of most Western evolutionists" (GOULD and ELDREDGE, 1977, p. 147). A recent report states that, "Evolution, according to the Modern Synthesis, moves at a stately pace, with small changes accumulating over periods of millions of years ..." (LEWIN, 1980, p. 883).

For examples of the gradualist bias in evolutionary theory, ELDREDGE and GOULD (1972) go back to Darwin, and cite in addition several older textbooks published in 1900, 1946 and 1952. They also (1977) give examples of a gradualist bias in modern paleontological research publications. However, their characterization of thinking in modern evolutionary theory is inaccurate. Let me briefly trace a line of thought in evolutionary theory that has been developing over the last 50 years.

In 1931 WRIGHT argued that the selection-drift combination could bring about exceptionally rapid evolutionary changes in colonial population systems (WRIGHT, 1931, 1949, 1960). This was later termed the shifting balance process (WRIGHT, 1978, 1980).

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[1]) KAREN A. GRANT read the manuscript critically, and Prof. Dr. RIGOMAR RIEGER prepared the German summary. I am grateful for their help.

[2]) This paper is dedicated to Prof. HANS STUBBE on his 80th birthday.

In 1944 SIMPSON proposed the model of quantum evolution in macroevolution from both paleontological evidence and population-theoretical considerations (SIMPSON, 1944, 1953).

In 1947 RENSCH (1947) discussed the explosive phase in the history of most large animal groups and in many smaller groups. He provided numerous examples and discussed the causes, emphasizing selection at specially high intensities (RENSCH, 1947, 1954, 1959).

In 1954 MAYR put forward the model of speciation and genetic revolutions in isolated peripheral founder populations (MAYR, 1954, 1963, 1970). In 1963 I took up MAYR's model of speciation, developed it further by adding the selection-drift factor to it and relating it to quantum evolution, and called it quantum speciation (GRANT, 1963, 1971, 1977b). Similar ideas were put forward under other terms by LEWIS and RAVEN (1958), LEWIS (1962) and CARSON (1971, 1975). LEWIS used the term speciation by catastrophic selection, and CARSON the term speciation by population flush-crash cycles.

The model of quantum speciation was placed in the context of macroevolution in 1963. It was suggested then that many evolutionary trends could be the resultant of series of quantum speciational events (GRANT, 1963, 1971). Trends of this sort were later named speciational trends (GRANT, 1977a, 1977b).

ELDREDGE and GOULD cite very little of the literature listed in the preceding paragraphs. The main influences in the field of evolutionary theory in ELDREDGE and GOULD (1972) appear to be MAYR and DARWIN. There is nothing in the 1972 paper to indicate that the authors are familiar with modern evolutionary theory apart from MAYR (1963). The 1977 paper (GOULD and ELDREDGE, 1977) is slightly better, in that it brings SIMPSON (1944, 1953) and CARSON (1975) into the discussion, but is still woefully deficient in its presentation of the relevant background literature.

To summarize this section, saltatory theories of evolution were popular in the early decades of this century before the synthetic theory was developed. Within the framework of the synthetic theory, a search for mechanisms that can bring about rapid and drastic evolutionary changes on an occasional or sporadic basis has been a continuing theme for 50 years. I cannot think of any major evolutionist in recent times who has advocated phyletic gradualism exclusively.

Punctuated Equilibria

According to the punctuated equilibrium model, evolutionary changes are concentrated in bursts corresponding to speciational events, separated by relatively long periods of evolutionary stagnation or stasis. "The history of evolution is not one of stately unfolding, but a story of homeostatic equilibria, disturbed only 'rarely' ... by rapid and episodic events of speciation" (ELDREDGE and GOULD, 1972, p. 84). "The history of life is more adequately represented by [this] picture of 'punctuated equilibria' than by the notion of phyletic gradualism" (op. cit., p. 84).

Furthermore, the separate speciational events can be linked in series to form evolutionary trends; and conversely, evolutionary trends are generally punctuational rather than gradualistic in nature (ELDREDGE and GOULD, 1972; GOULD and ELDREDGE, 1977).

The idea of punctuated equilibria has been presented as new (ELDREDGE and GOULD, 1972; GOULD and ELDREDGE, 1977) and even revolutionary (LEWIN, 1980). Certainly the term is new. As to the idea, let us try to put it in historical perspective by going over once again the series of concepts presented in the preceding section.

WRIGHT's selection-drift concept and shifting balance theory postulate episodes of rapid change within species populations over relatively short time periods. This is a microevolutionary concept. It has an obvious bearing on macroevolution, however, and has influenced later evolutionists dealing specifically with macroevolution.

SIMPSON's concept of quantum evolution puts the earlier Wrightian concept of the role of small populations squarely into the realm of macroevolution. Changes in morphology and shifts to new adaptive zones are held to take place rapidly in small populations, and this can explain the rarity of transitional forms in the fossil record. By contrast, the large populations existing before and after the quantum shifts, which may be well represented in the fossil record, exhibit normal or slow evolutionary rates (SIMPSON, 1944, 1953).

Macroevolution thus occurs in pulses or episodes. "The quantum change is a break-through from one position of stabilizing selection to another" (SIMPSON, 1953, p. 391).

SIMPSON (1944, 1953) presents quantum evolution as a special mode coordinate with speciation on the one hand and phyletic evolution on the other. "It may be involved in either speciation or phyletic evolution ... [but it] also occurs on a larger scale and in clear distinction from any usual phase of speciation and phyletic evolution (SIMPSON, 1944, p. 206). A later treatment states, "It is a special, more or less extreme and limiting case of phyletic evolution;" but new species and higher groups may also "often arise in this way" (SIMPSON, 1953, p. 389). Thus quantum evolution does not necessarily involve speciation, but it may.

There are some differences between the 1944 and 1953 versions of quantum evolution. The latter, for example, is more conservative as regards possible inadaptive transitional phases. However, these and other differences are peripheral to our central theme here.

MAYR's (1954) model of drastic changes, or genetic revolutions, in isolated peripheral populations also makes use of the special properties of small populations. In MAYR's model the changes are definitely speciational and can be of macroevolutionary magnitude.

Although the rapid changes take place in small populations, MAYR ascribes them to his own previously described founder effect rather than to drift or selection-drift, which he regards as different (MAYR, 1954; 1963, p. 209); but it can be shown that the founder effect is a special case of drift. Also MAYR (1954) makes only passing mention of quantum evolution, although MAYR's mode of speciation seems to be related to quantum evolution. In any case, it is an important mode of speciation with macroevolutionary potential.

With these considerations in mind, I later called the process quantum speciation and identified the evolutionary forces behind it as selection-drift (GRANT, 1963, pp. 456–459).

Later in the same work, in discussing evolutionary trends, I suggested that some trends may be the result of phyletic evolution or anagenesis, i. e., intraspecific changes, but other trends might represent series of speciational shifts (GRANT, 1963, pp. 563–568). "It is contended that evolutionary trends, in some cases, are the resultant of a stepwise succession of divergences ..." (op. cit., p. 566).

Now if quantum speciation can bring about a rapid adaptive response once it can do so repeatedly. A series of quantum speciational events might be the most successful response of a phylad to a strong environmental challenge. "The evolutionary trend in a very rapidly changing environment or toward a remote adaptive goal is thus considered to be a succession of quantum speciational changes ..." (op. cit., p. 567). Such a succession would usually be indistinguishable in the fossil record from a strictly phyletic or anagenetic trend.

The term speciational trend was introduced later for such series for clarity and to distinguish them from conventional phyletic trends (GRANT, 1977a).

ELDREDGE and GOULD do not discuss the relevant previous concepts outlined above with the single exception of MAYR's mode of speciation. The punctuated equilibrium concept is very similar to the quantum evolution concept. One would expect ELDREDGE and GOULD to compare the two, but they do not do this. It is amazing that they do not mention quantum evolution at all in their 1972 paper and only once, and that in an incidental way, in their 1977 paper. ELDREDGE and GOULD's suggestion about the role of speciation in evolutionary trends is essen-

tially the same as the one I put forward in 1963, and one could expect some cross-comparisons here too, but they ignore the 1963 suggestion completely.

Is Punctuational Evolution the Norm?

ELDREDGE and GOULD (1972, 1977) consider the punctuational model to represent the norm and phyletic gradualism to be rare. "We believe that punctuational change dominates the history of life ... phyletic gradualism is very rare and too slow, in any case, to produce the major events of evolution" (GOULD and ELDREDGE, 1977, p. 115).

In their 1977 paper they reanalyze some 15 previously published paleontological studies in which evolutionary trends can be discerned. Phyletic gradualism has been assumed in nearly all of these cases. GOULD and ELDREDGE (1977) conclude that gradualism is dubious for most of the examples in this sample. In their judgment only one good, or possibly good, case of phyletic gradualism is found, in the Permian foraminifer *Lepidolina* (OZAWA, 1975).

Their interpretation of the fossil record is not accepted by some other paleontologists who have dealt with the same data (e. g., GINGERICH, 1976, 1977). There *is* paleontological evidence for gradual changes within a species lineage in a fair number of cases.

I believe that ELDREDGE and GOULD may be underestimating the role of phyletic gradualism, and that their way of formulating the problem leads to such an underestimate. They set up a dichotomy between rapid punctuational change and stasis. Most evolutionists would regard these two conditions as the extremes in a spectrum of evolutionary rates. But ELDREDGE and GOULD use them as contrasting conditions; a lineage is in either one state or the other.

ELDREDGE and GOULD equate punctuational change with MAYR's mode of speciation ("allopatric speciation" in their misleading terminology; quantum speciation in ours). And they regard quantum speciation as the main speciation mode (1972, p. 94). Stasis, on the other hand, is abundantly documented in the fossil record; in fact, paleontological evidence is heavily biased in favor of stasis. Stasis can be observed; the unobserved non-stasis is attributed to punctuational change mediated by quantum speciation.

However, ELDREDGE and GOULD have a grip on only a small part of the large complex subject of speciation in recent organisms. Geographical speciation, which they dismiss, takes place too and is slow. A large species population is not necessarily confined to stasis or only minor changes when long-continued selective pressures are involved (contra GOULD and ELDREDGE, 1977, pp. 115, 117). Phyletic evolution and phyletic trends are not necessarily rare (contra GOULD and ELDREDGE, 1977, p. 115).

ELDREDGE and GOULD (1972, 1977) try to put down the classical argument for gradualism based on the incompleteness of the fossil record. They perhaps try too hard in this. One gets the impression that they feel that the stratigraphic gaps have been used on behalf of phyletic gradualism for over a century, and now the punctuational model should have its turn to use the gaps. It is, of course, hazardous to lean very much on negative evidence for either side of this question. The gaps in the record are consistent with the punctuational model, but, in many or most cases, they are not inconsistent with gradualism either.

In my treatment of the problem in 1963 I recognized four general modes: (1) stasis in a bradytelic lineage; (2) slow phyletic evolution; (3) a trend progressing at moderate rates mediated by a combination of speciational and phyletic changes; and (4) a rapid evolutionary trend composed of a series of quantum speciational shifts. These modes could be related to the type of environmental challenge: (1) long-continued stable environment; (2) slowly and progressively changing environment; and (3) moderately or (4) rapidly changing environment. The different modes of environmental stability or change undoubtedly exist. And the surviving

lineages are those which are able to make the appropriate response to their type of environment (GRANT, 1963, pp. 542 ff.). This scheme provides for a greater diversity of macroevolutionary patterns than does the punctuational model.

In summary, I agree with ELDREDGE and GOULD (1972, 1977) that speciation probably plays a more important role in macroevolution than has been thought in the past, but I have to disagree with them on a number of subsidiary questions.

Directed Speciation and Species Selection

The punctuational model has been advocated and developed more or less independently by STANLEY in a series of publications including one important book (STANLEY, 1975, 1977, 1979; RAUP and STANLEY, 1978). STANLEY's views and conclusions are similar in general to those of ELDREDGE and GOULD presented above. Consequently a detailed account of them is unnecessary here. STANLEY's style of presentation, however, is different from that of ELDREDGE and GOULD. In style, STANLEY's book (1979) is scholarly, well documented, and gives proper credit to previous studies in evolutionary theory; and in substance it makes a strong case for the punctuational model.

I wish to discuss briefly certain points made by STANLEY regarding speciation. The first of these is species selection. STANLEY characterizes it as follows: "Whereas, natural selection operates upon individuals within populations, a process that can be termed *species selection* operates upon species within higher taxa, determining statistical trends" (STANLEY, 1975, p. 648, italics in original; cf. also 1979, pp. 186 ff.). GOULD and ELDREDGE (1977, p. 139) referred to species selection as a "previously unrecognized mode of operation for natural selection ..." STANLEY himself (1975, p. 648) presents it as newsy rather than new.

This process, under the term interspecific selection, has long been known in ecology, and has been discussed by a number of evolutionists. One can think of the classical experiments of GAUSE with *Paramecium* in the 1930's and those of PARK with *Tribolium* in the 1940's.

The assumption that species selection is a new or at least newsy concept is a contributing factor to STANLEY's (1979) misunderstanding of my views of 1963 on speciational trends. He reinterprets the process as "directed speciation, ... a tendency for speciation to move in one adaptive direction, " and contrasts it with trends due to species selection (STANLEY, 1979, pp. 183, 193).

I have never believed in or described any process of directed speciation sensu STANLEY. My original (1963) discussion of speciational trends was preceded by one chapter devoted mainly to interspecific selection and other chapters that brought out the opportunism of the speciation process. The discussion of trends was built on these foundations. My views were amplified later (GRANT, 1977a, 1977b, cf. also 1971). The directedness in speciational trends was attributed by me in both 1963 and 1977 to interspecific selection operating along an environmental gradient.

STANLEY (1975, 1979) advocates the idea that speciation has "a strong random element" (1979, p. 186) ..." In fact, the process of speciation is to a large extent random" (STANLEY, 1975, p. 648). "Randomness refers to the *direction* of speciation events ... (STANLEY, 1979, p.189, italics in original)."... I stress that *it is quite possible for directions of speciation within a clade to be randomly determined even if evolution is guided solely by natural selection*" (op. cit., p. 189, italics in original). GOULD and ELDREDGE (1977) also support this view. All three authors draw a loose analogy between the role of speciation in macroevolution and that of mutations in microevolution.

In my opinion the notion of randomness as applied to speciation is misleading; it is as wrong as the notion of directed speciation. The claim of randomness in speciation ignores the ecological constraints in nature. The speciation process is not completed until a daughter species is established in some natural community. And competitor species are normally already established there. Individuals and populations that could, potentially, become daughter species will often arise but be suppressed by superior preexisting competitor species. The only actual new daughter species will be those that are adapted to and occupy a niche in which they are competitively superior. The speciation process is neither random nor directed, but opportunistic.

The results of the speciation process are controlled ecologically. The only products to actually develop, among the many unsuccessful probes and false starts, are those that can and do exploit an ecological opportunity. This is the opportunistic aspect of speciation. And if, as often happens, the ecological opportunities in nature are lined up in the form of an environmental gradient, so that a speciational shift to a more extreme environment is the only available way to go, then a trend can develop in a series of daughter species, a speciational trend.

Stanley (1975, 1979) also advocates the hypothesis that evolutionary trends may be built up from speciational events. He regards such trends as products of random speciation and species selection. Here the difference between our positions is relatively small. Whereas in Stanley's formulation the trend is a product of random speciation and species selection, in mine it is a product of opportunistic speciation and interspecific selection.

Other Views

A list is given here of some other recent papers, pro and con, on the punctuational model. The list is not complete. There is very little overlap between the present paper and the others listed. I am critical of the punctuational equilibrium theory; but I agree with parts of it too; and on those parts I disagree with some other critics of punctuational equilibria.

Recent accounts favorable to the punctuational model are given by Lewin (1980) and Vrba (1980). Vrba presents an interesting review.

Recent criticisms are those of Hecht (1974), Gingerich (1976, 1977), White and Harris (1977), Levington and Simon (1980), Templeton (1980), and Futuyma et al. (1981).

Stanley (1975, 1979) cites papers of Ruzhentsev (1964), Nevesskaya (1967), and Ovcharenko (1969) as forerunners of punctuationalism. Raup and Stanley (1978, pp. 324–325) give a summary of their views. I have read these papers with interest but I do not get the same message from them that Raup and Stanley do.

Ruzhentsev (1964) gives a very general discussion of phylogenetic patterns, and touches briefly on gradual changes vs. discontinuity, but does not expand on or endorse either alternative. He devotes more attention to the species problem in phylogeny. Nevesskaya (1967) likewise is mainly concerned with the species problem in paleontology.

Ovcharenko (1969) comes closer to a punctuational view on the basis of his work with a Jurassic brachiopod, *Kutchithyris*. An ancestral species *K. acutiplicata* and a descendant species *K. euryptycha* are connected by transitional forms in an intermediate layer. The duration of the two species is inferred to be long and that of the transitional forms short. The rapid establishment of the new species contrasts with its relatively stable existence thereafter (Ovcharenko, 1969). However, we don't know whether *K. acutiplicata* and *K. euryptycha* form a pair of biological species or a pair of paleospecies. Consequently, the facts in this case are consistent with various models. A quantum speciational shift is a definite possibility, but so is quantum evolution within a phyletic lineage.

Conclusions

A satisfactory theory of macroevolution must be consistent with the fossil evidence and with our knowledge of microevolutionary processes. Due to the incompleteness of the fossil record and the diversity of microevolutionary processes, these two conditions are not completely restrictive. The conditions are flexible enough to permit more than one "satisfactory" theory of macroevolution.

During the last four decades the synthetic theory of evolution has given an account of macroevolution which has seemed adequate to many evolutionary biologists. This theory has never been monolithic; different shades of opinion have been held on macroevolution (and other questions) by its exponents. Recently the synthetic theory has been challenged by the punctuational equilibrium theory (1972, 1975, 1977, 1979, for dates of key publications). The challenge is accompanied by a considerable amount of controversy.

The tenets of the punctuational model can be summarized as follows: (1) Species lineages during most of their history are static and unchanging or nearly so. The species population is incapable of significant sustained evolutionary response to selective pressures. (2) Most evolutionary change is concentrated in bursts corresponding to speciational changes. (3) Evolutionary trends are made up of series of such speciational shifts. (4) The punctuational model stands in contrast to a model of phyletic gradualism, which is attributed to the synthetic theory.

The authors of the punctuational theory are wrong as regards point 4. Although phyletic gradualism does have a place in the synthetic theory, a bigger place in some versions than in others, it does not occur there to the exclusion of occasional evolutionary bursts. The authors of the punctuational model are tilting at a straw-man of their own creation.

Point 1 involves both a statement of observation in paleobiology and an assumption about microevolutionary dynamics. Species stasis is certainly well documented in the fossil record. The paleontological evidence, in fact, is biased in favor of static species. There is no basis in microevolution, however, for denying the possibility of gradual intraspecific changes. Furthermore, species lineages exhibiting gradual changes through time are not rare or exceptional in the fossil record. The authors of the punctuational theory underestimate the theoretical possibility and the probable frequency in phylogeny of strictly phyletic or anagenetic change.

Points 2 and 3 are tenets of common versions of the synthetic theory. A forerunner of point 2, quantum evolution, was proposed in 1944 and 1953; a concept similar to point 2, quantum speciation, was proposed in 1954 and 1963; and a concept synonymous with point 3, speciational trends, was stated in 1963 (and later). These earlier statements from exponents of the synthetic theory have mostly been ignored or misunderstood by the authors of the punctuational theory. Nevertheless, the published record shows that the punctuational theory has been anticipated in these essential points.

The main positive result of the punctuational theory so far, in my opinion, is the focusing of attention on speciation in macroevolution. A significant macroevolutionary role of speciation had been suggested earlier within the synthetic theory, as noted above, but had not received much attention. This situation has undergone a change for the better with the advent of the punctuational equilibrium model.

The most likely conclusion that we can draw at present about macroevolutionary change is that it takes place by various pathways: as slow phyletic trends, rapid speciational trends, and mixtures of these.

Zusammenfassung

„Punctuated Equilibria": Eine Kritik

Eine zufriedenstellende Theorie der Makroevolution muß mit den fossilen Befunden und dem Wissen um die Mikroevolution in Einklang stehen. Auf Grund der Unvollständigkeit der fos-

silen Daten und der Vielzahl mikroevolutionärer Prozesse sind diese beiden Bedingungen nicht vollständig zwingend zu erfüllen. Diese Sachlage erlaubt es, mehr als eine „zufriedenstellende" Theorie der Makroevolution zuzulassen.

Während der vergangenen vierzig Jahre hat die synthetische Theorie der Evolution eine vielen Evolutionsbiologen adäquat erscheinende Darstellung der Makroevolution gegeben. Diese Theorie war jedoch nie „monolitisch"; verschiedene Exponenten vertreten durchaus nicht völlig übereinstimmende Vorstellungen. In jüngster Zeit ist die Gültigkeit der synthetischen Theorie durch die Theorie des "punctuational equilibrium" in Frage gestellt worden. Gleichzeitig damit wurden in erheblichem Umfang Kontroversen ausgelöst.

Die Hauptinhalte des "punctuational" Modells lassen sich wie folgt zusammenfassen:

1. Species-Folgen sind im Verlauf ihrer Geschichte meist statisch und unterliegen nur geringem Wandel. Die Species-Population ist nicht imstande, auf Selektionsdruck über lange Zeiträume mit evolutionären Reaktionen zu antworten.
2. Die meisten evolutionären Veränderungen erfolgen in Form von rapiden Art-Veränderungen.
3. Evolutionäre Trends bestehen aus Serien derartiger Species-Verschiebungen.
4. Das "punctuational" Modell steht im Gegensatz zur Theorie des phyletischen Gradualismus, die der synthetischen Theorie der Evolution zugeschrieben ist.

Die Verfechter der "punctuational theory" vertreten eine falsche Position in Bezug auf Aussage 4. Obgleich der phyletische Gradualismus einen Platz im Rahmen der synthetischen Theorie der Evolution findet, schließt er keineswegs gelegentliche und dabei „rapide" evolutionäre Fortschritte aus. Die Autoren des "punctuational model" schlagen auf einen Strohmann eigener Schöpfung ein.

Punkt 1 beinhaltet sowohl paläobiologische Beobachtungen als auch Annahmen zur mikroevolutionären Dynamik. "Species-Stasis" ist durch Untersuchungen fossilen Materials natürlich gut belegt. In der Tat deuten Befunde an fossilem Material einseitig auf den statischen Charakter der Species hin. Die Mikroevolution gibt jedoch keinen Anlaß, graduelle intraspezifische Veränderungen zu verleugnen. Darüber hinaus sind Species-Folgen, die graduelle Veränderungen im Laufe der Zeit erfahren, keineswegs selten oder stellen etwa nur Ausnahmefälle unter den auf fossile Daten gegründeten Befunden dar. Die Autoren der "punctuational theory" unterschätzen die theoretische Möglichkeit und wahrscheinliche Häufigkeit streng phyletischer oder anagenetischer Veränderung in der Phylogenie.

Die Punkte 2 und 3 sind Gesichtspunkte, die Bestandteil der synthetischen Theorie der Evolution sind. Ein Vorläufer der in Punkt 2 getroffenen Feststellung ist die Quantumevolution, die 1944 und 1953 als Vorgang begründet wurde. Ein der Quantumevolution ähnliches Konzept, die Quantum-Speciation, wurde 1954 und 1963 eingeführt. Ein Konzept, das mit Punkt 3 synonym ist, die sog. "speciational trends", wurde 1963 (und später) entwickelt. Diese frühen Feststellungen von Vertretern der synthetischen Theorie werden von den Verfechtern der "punctuational theory" entweder nicht berücksichtigt oder falsch verstanden. Unbeschadet dessen weisen die vorliegenden Publikationen aus, daß Inhalte der "punctuational theory" in wesentlichen Punkten bereits vorformuliert worden sind.

Nach Meinung des Verfassers ist das wichtigste positive Ergebnis der "punctuational theory", daß die Aufmerksamkeit auf die Rolle der Artbildung bei der Makroevolution gelenkt wird. In der Tat wurde auch im Rahmen der synthetischen Theorie der Artbildung eine wesentliche Rolle zugebilligt, aber diese Ableitung stieß nicht auf die erforderliche Resonanz. Mit der Formulierung des "punctuational equilibrium model" hat sich diese Situation zum Besseren entwickelt.

Die beste Schlußfolgerung, die sich derzeit zum Problem makroevolutionärer Veränderung

ziehen läßt, ist daß sie über verschiedene Wege erfolgt: in der Form langsam verlaufender phyletischer Trends, in Form relativ schneller Artbildung-Trends und als Mischung beider Vorgänge.

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Das nunmehr in 2., nahezu unveränderter Auflage vorliegende Werk vereinigt in fast idealer Weise Grundelemente eines Lehrbuches mit denjenigen eines phytopathologischen Praktikums und eines Atlas wichtiger Pflanzenkrankheiten. Es sind biologische und phytopathologische Grundkenntnisse, diagnostische und experimentelle Aspekte mit großem didaktischem Geschick und einem ausgezeichneten Blick für das Wesentliche zu einem harmonischen Ganzen gefügt. Eingangs werden prägnant Grundbegriffe der Phytopathologie definiert. Es folgen ausgezeichnet illustrierte Hinweise zur Interpretation mikroskopischer Beobachtungen. Ein Abschnitt über Grundlagen der Steriltechnik beschließt die allgemeinen Ausführungen. Doch auch in den folgenden, vorzüglich illustrierten 52 Abschnitten, in denen Bakteriosen, Virosen und Mykosen in guter, der Pathogensituation der USA Rechnung tragender Auswahl abgehandelt werden, erfolgt die Vermittlung weiterer phytopathologischer Grundkenntnisse, wobei diese an konkreten Beispielen demonstriert werden. In diesen speziellen Abschnitten folgt auf einführende grundlegende Bemerkungen die Symptombeschreibung. Diese wird durch eine Folge von Fotografien unterstützt, in der die erkrankte Pflanze im Ganzen und spezifische Symptome in Großaufnahmen gezeigt werden. Oft werden diesen ähnliche, durch anderweitige Ursachen bedingte Krankheitsbilder gegenübergestellt. Es folgen Mikrophotographien von Schnitten und oft nach diesen angefertigte Zeichnungen. Ein Diagramm zum Lebenszyklus des Pathogens vervollständigt in der Regel die Ausführungen. Abschließend werden Bekämpfungsmaßnahmen erörtert. Detaillierte Hinweise auf erforderliches Pflanzen- und Pathogenmaterial und anderweitige experimentelle Erfordernisse erleichtern die Planung und Durchführung entsprechender Kurse. Diskussionsfragen und Hinweise auf weiterführende Literatur regen den Studenten zu vertiefenden Studien an. Der Wert des in der Konzeption und im Aufbau geradezu faszinierenden und unter Berücksichtigung der ausgezeichneten Ausstattung ausgesprochen preiswerten Buches wird allerdings dadurch geschmälert, daß in der 2. Auflage lediglich kleinere Unebenheiten der ersten Auflage beseitigt worden sind. Neue Erkenntnisse, die in den 11 zwischen dem Erscheinen der 1. und 2. Auflage vergangenen Jahren gewonnen worden sind, bleiben unberücksichtigt. So werden beispielsweise durch Mykoplasmen hervorgerufene Krankheiten, z. B. die infektiöse Vergilbung der Aster, noch immer als Beispiele für Viruskrankheiten abgehandelt. Selbst revolutionierende Fortschritte in der Bekämpfung von Pflanzenkrankheiten, wie sie z. B. durch die Entwicklung der systemischen Fungizide (Vektorenbekämpfung) erzielt worden sind, bleiben unerwähnt. Die Literaturhinweise bleiben auf die vor 1968 erschienenen Veröffentlichungen beschränkt. Der mit dem Buch arbeitende Student benötigt daher die weiterführende Unterstützung durch erfahrene Hochschullehrer.

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